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CYLINDROPUNTIA CHUCKWALLENSIS (CACTACEAE), A NEW SPECIES FROM RIVERSIDE AND IMPERIAL COUNTIES, CALIFORNIA

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ABSTRACT

A gynodioecious hexaploid ($n = 33$), ***Cylindropuntia chuckwallensis*** M. A. Baker & M. A. Cloud-Hughes, is newly described. Populations of *C. chuckwallensis* extend from the Eagle Mountains of Joshua Tree National Park, through the Chuckwalla Mountains of Riverside County, to the north side of the Chocolate Mountains in Imperial County, California, USA, and occur on a variety of substrates primarily between 400–1600 m (1312–5250 ft) elevation. Of the flowering individuals studied, 38% produced only pollen-sterile flowers. Flower color in *C. chuckwallensis* ranges from dark red-purple (33%) through orange (54%) to yellow (13%). For most individuals (93%) the style and filaments are dark red to light pink. Morphological measurements were made for 15 populations of *Cylindropuntia*, including four of *C. chuckwallensis*, four of *C. echinocarpa*, three of *C. multigeniculata,* and four of *C. acanthocarpa*. Multivariate analyses indicated that *C. chuckwallensis* possesses a unique combination of characters. Fewer than 3% of the 121 *C. chuckwallensis* individuals sampled were misclassified by discriminate function analysis, one as *C. echinocarpa,* and three as *C. multigeniculata*.

Key Words: *Cylindropuntia chuckwallensis*, Cactaceae, endemism, evolution, gynodioecy, new species, polyploidy, speciation.

The study of *Cylindropuntia* (Engelm.) F. M. Knuth continues to engage biologists attempting to understand the origins and relationships of its taxa and their underlying evolutionary mechanisms. Common processes associated with the genus include eupolyploidy, hybridization, and apogamy (Baker and Pinkava 1987). Aneuploidy appears to be rare in Cactaceae and has not been documented in *Cylindropuntia* (Baker et al. 2009). Vegetative reproduction is common and is the only form of apogamy recorded for the genus. However, adventive embryony has been reported for *Opuntia* Desv. (Davis 1966) and may be responsible for the primary mode of reproduction in some species such as the pentaploid allopolyploid *O.* × *charlestonensis* Clokey (pro. sp.) (Beard 1937; Baker et al. 2009).

There are several hexaploid species known for *Cylindropuntia.* These include *C. arbuscula* (Engelm.) F. M. Knuth, *C. calmalliana* (J. M. Coult.) F. M. Knuth, *C. sanfelipensis* (Rebman) Rebman, and *C. wolfii* (L. D. Benson) M. A. Baker (Pinkava and McLeod 1971; Pinkava et al. 1992, 1998). All of these, except *C. arbuscula* which is largely, if not entirely, clonal, are gynodioecious (Rebman 1998; Rebman and Pinkava 2001) with some individuals having perfect flowers and others having pollen-sterile flowers. One primarily octoploid species, *C. molesta* (Brandegee) F. M. Knuth, is also gynodioecious (Pinkava et al. 1998; Rebman and Pinkava 2001).

Correlation between polyploidy and subdioecy has also been observed in other cactus genera. Most *Consolea* Lem. species, for example, are both hexaploid and subdioecious (Negrón-Ortiz 2007). In *Echinocereus* Engelm. and *Mammillaria* Torr. & A. Gray, subdioecy is associated only with tetraploid and hexaploid taxa (Remski 1954; Johnson 1980; Parfitt 1985; Pinkava et al. 1985, 1998; Baker 2006). However, at least two *Opuntia* taxa, *O. stenopetala* Engelm. and *O. grandis* Pfeiff., are diploid and subdioecious. Thus, at least in some cactus genera, gender dimorphism has been documented only for polyploids, with the majority of subdioecious taxa being hexaploid. Selection pressure for floral dimorphism may be greater in polyploids because of a decrease in self-incompatibility (Marks 1966). Male-sterile mutants may be favored as a response to inbreeding depression resulting from this reduction in self-incompatibility (Miller and Venable 2000). Pressure for outbreeding is also a logical consequence for an almost certainly low population size for incipient allopolyploids.

We herein describe a new hexaploid gynodioecious *Cylindropuntia* species, *Cylindropuntia chuckwallensis* M. A. Baker & M. A. Cloud-Hughes, from the Chuckwalla Mountains region of Riverside and Imperial counties, California, and test the significance of differences among mean values for certain morphological characters among populations of this new species and the two most morphologically similar species, *C. echinocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth and *C. multigeniculata* (Clokey) Backeb. Populations of *C. acanthocarpa* have been included as an outgroup.

Populations of *Cylindropuntia multigeniculata* have been referred to as a nothospecies, *C.* × *multigeniculata* Backeb. (Pinkava 1999, 2003), with the putative parents being *C. echinocarpa* and *C. whipplei* (Engelm. & J. M. Bigelow) F. M. Knuth. However, the determination of hybrid status was made without supporting data and disregarded data from Trushell (1985). Some of the confusion lies in the identification by Pinkava (2003) as compact forms of *C. echinocarpa* of what we now consider to be Arizona populations of *C. multigeniculata* (Baker 2002). Except for the somewhat spinier fruits, the Arizona individuals are morphologically similar to those at the type locality of *C. multigeniculata*. Populations of *C. multigeniculata* possess several characters that are not intermediate between those of the putative parents, and the means of these characters are significantly different from those of either of the putative parents.

Morphologically, the effects of hybridization within the Opuntioideae appear to be additive. Milhalte and Sestras (2012) found a range of heritability between 0.909 and 0.948 among a suite of morphological characters for F_1 individuals of artificial hybridization within Cactaceae, indicating that the characters analyzed had a strong genetic determinism. Statistical analyses of natural cactus hybrids have had similar results, where the morphology of hybrids exhibits the expected degree of intermediacy between that of putative parents (Baker and Pinkava 1984; Powell et al. 1991; Vite et al. 1996; Powell and Weedin 2004). However, with respect to hybridization in Cactaceae, flower pigmentation appears to be less predictable (Powell 2002).

Specimens of *Cylindropuntia chuckwallensis* have been identified historically as *C. echinocarpa*. Philip Munz, David Keck, and M. French Gilman collected samples of *C. chuckwallensis* at Corn Springs in 1922 (POM11971, POM13960), while Willis L. Jepson (JEPS66875) and Frank Peirson (RSA65624) collected samples at Cottonwood Springs on consecutive days in 1928, with Peirson noting the "peculiar dull reddish purple" of the flowers on the herbarium label.

MATERIALS AND METHODS

Fieldwork was conducted between May 2011 and May 2013. Figure 1 presents an overview of the study sites for *Cylindropuntia chuckwallensis*, and descriptions of all study sites are presented in Table 1. Samples of 30–35 individuals were measured for each population. In studies of the Cactaceae, 30 individuals account for approximately 90% of the variation within most characters in a single population and provide a good balance between field effort and statistical robustness (Baker and Butterworth 2013). In order to account for geographical effects, we suggest that at least three populations be sampled for any putative taxon and that these populations be spread over the geographical range as widely as possible. This precept stems from the fact that geographically isolated populations, even within the same taxon, often have a rather uniform morphology. With discriminant analyses, individuals within such populations are sometimes classified correctly for that population nearly 100% of the time. If all such populations were recognized as separate taxa, the number of taxa within the Cactaceae would be unmanageable. Thus, this type of analysis may not be suitable for potential taxa with only one or two known populations or with only a few known individuals. We define a population here as a collection of individuals that, as far as can be determined, exchange genes frequently among themselves but rarely, if ever, exchange genes with other populations.

In addition to the four populations sampled for our new taxon, we also sampled five populations of *Cylindropuntia acanthocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth, four populations of *C. echinocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth, and three populations of *C. multigeniculata* (Clokey) Backeb. *Cylindropuntia acanthocarpa* was sampled as a morphological outgroup. Populations of *C. echinocarpa,* which are sympatric with the new species, and those of *C. multigeniculata*, which are allopatric, were included because of their morphological similarity to the new species.

Thirteen stem characters were measured for 452 individuals among the 15 populations (Table 2). It was assumed that all individuals within a single population belong to a single taxon except for the co-existing populations of *C. acanthocarpa* and *C. echinocarpa* west of Needles, California, and the Joshua Tree National Monument and Graham Pass Road populations of *C. chuckwallensis*, where there were a few easily-distinguished individuals of *C. echinocarpa*. All characters were measured three times per individual, and the values for each character were averaged before any statistical analyses were performed. Spine and sheath thick-

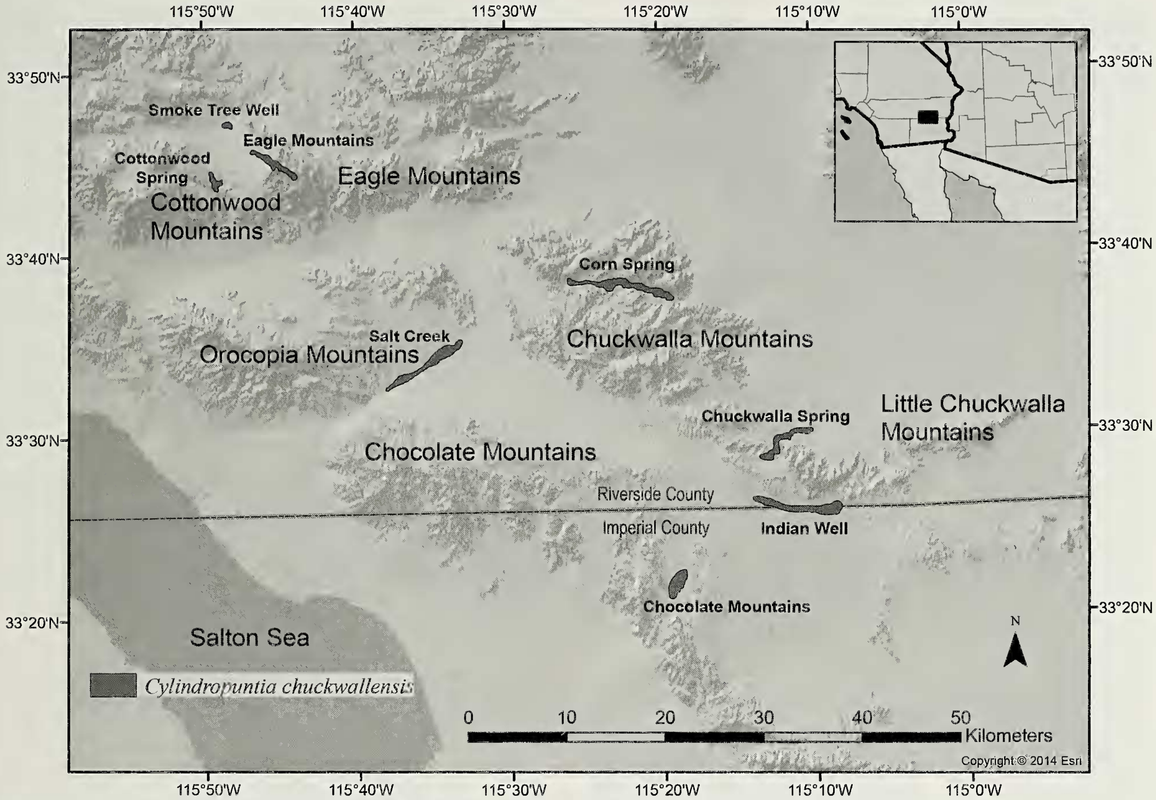

FIG. 1. Geographic distribution of *Cylindropuntia chuckwallensis* and locations of study sites.

nesses were measured to the nearest 0.01 mm using digital calipers. Repeated measurements were performed to increase the number of possible values for each character. Data were then imported into Systat® 10 (Systat Software, Inc., Chicago, IL), SPSS® 12 (IBM, Inc., Armonk, NY), and NTSYSPC® (Exeter Software, Setauket, NY). Discriminate function analysis (DFA) was performed to ascertain the correct classification of individuals for each taxon, and MANOVA was used to determine which character means differed significantly among the various taxa.

RESULTS

Field surveys indicate that populations of *Cylindropuntia chuckwallensis* are restricted to areas in and around the Chuckwalla Mountains of Riverside County, California. To date, the known northern extent of the species is in the Eagle Mountains of Joshua Tree National Park, and the southern extent is on the north side of the Chocolate Mountains in the northernmost portion of Imperial County (Fig. 1). The total range is approximately 50 km north to south and 60 km east to west. There are approximately 3200 hectares of known occupied habitat for *C. chuckwallensis*. Although densities of individuals are as high as five or more individuals per hectare, the average density is probably closer to 2.5 individuals per hectare.

Cylindropuntia chuckwallensis is apparently gynodioecious. Of 151 individuals observed in flower, 38.4% produced only pollen-sterile flowers, and 61.6% produced only pollen-fertile flowers, with pollen-fertile individuals producing seeds. Flower color ranged from dark red-purple (33.1%) through orange (54.3%) to yellow (12.6%). For most individuals (92.7%), the style and filaments were dark red to light pink, at least toward their apices (Fig. 2).

Chromosome determinations of $n = 33$ were made for 13 individuals of *Cylindropuntia chuckwallensis*; and $n = 11$ for one individual of *C. acanthocarpa*, one individual of *C. echinocarpa*, and five individuals of *C. multigeniculata* (Table 1). One chromosome determination was made for an individual of *C. chuckwallensis* that was not associated with the sites listed in Table 1: California, Riverside County, along Salt Creek, 17.5 km WNW of Black Butte, 18 km SE of Chiriaco Summit, 33.5866°, −115.5521°, *M. A. Baker 17533* (ASU, UCR). A chromosome determination of $n = 11$ was made for two individuals (*M. A. Baker 15259* [ASU, RSA]; *M. A. Baker 15260* [ASU, US]) at sample site 11 (Table 1),

TABLE 1. LOCATIONS, PLOIDY LEVELS, SAMPLE SIZES (N), AND HERBARIUM VOUCHERS OF *CYLINDROPUNTIA* POPULATIONS SAMPLED FOR THE MORPHOLOGICAL ANALYSIS. Previously unpublished chromosome number vouchers and their respective vouchers are in bold. Other chromosome numbers are from Baker et al. (2009), Pinkava et al. (1992, 1998). ND = Chromosome count not determined. MAB = M. A. Baker, MCH = Michelle Cloud-Hughes.

Pop. site no.	Taxon	Chromosome number	Locality	N	Latitude, longitude	Elev. (m)	Voucher specimens
1	*C. chuckwallensis*	**$n = 33$**	CA, Riverside Co., Corn Springs Wash, N side of Chuckwalla Mts., 85 km E of Indio	30	33.6233° −115.3255°	500	***MAB 17525.1; MAB 17525.4; MAB 17525.6; MAB 17525.7;*** *MAB 17534; MAB 17535; MAB 17507; MAB 17510; MCH 087*
2	*C. chuckwallensis*	**$n = 33$**	CA, Riverside Co., 1.7 km NNE of Chuckwalla Spring, N side of Chuckwalla Mts., 57 km W of Blythe	30	33.4917° −115.2098°	500	***MAB 17536; MAB 17536.1***
3	*C. chuckwallensis*	**$n = 33$**	CA, Imperial Co., S side of Chuckwalla Mts., 3.8 km SW of Graham Pass, 3 km E of Indian Wells, 54 km WSW of Blythe	34	33.4271° −115.1492°	470	*MAB 17537;* ***MAB 17719.1; MAB 17719.2; MAB 17719.3; MAB 17719.4***
4a	*C. chuckwallensis*	**$n = 33$**	CA, Riverside Co., Cottonwood Mts., 450 m SW of Cottonwood Spring, 38 km NE of Indio	10	33.7336° −115.8131°	895	***MAB 17721.1;*** *Harding 134*
4b	*C. chuckwallensis*	**$n = 33$**	CA, Riverside Co., Eagle Mts., 800 m S of Smoke Tree Wash, 40 km NE of Indio	21	33.7856° −115.8041°	940	***MAB 17720.2; MAB 17720.3***
5	*C. echinocarpa*	$n = 11$	CA, San Bernardino Co., 9km WSW of South Pass, 32 km W of Needles, just S of Interstate 40 (neotype locality)	30	34.8375° −114.9848°	670	*MAB 13838; L. Benson 10374*
6	*C. echinocarpa*	**$n = 11$**	CA, Riverside Co., 1km N of Chiriaco Summit, 48 km E of Indio	33	33.671° −115.7220°	555	*MAB 17531;* ***MAB 17699.2***
7	*C. echinocarpa*	$n = 11$	CA, San Diego Co., Carrizo Valley, 1 km SE of Egg Mtn., 90 km E of central San Diego	30	32.8584° −116.2078°	210	*MAB 7531*
8	*C. echinocarpa*	$n = 11$	NV, Clark Co., S end of Blue Diamond Hill, just N of the town of Blue Diamond	30	36.0517° −115.4082°	1035	*MAB 13670*
9	*C. multigeniculata*	$n = 11$	NV, Clark Co., just N of Blue Diamond (type locality)	35	36.052° −115.396°	1240	*Clokey 8430; MAB 4969-A; MAB 11374A; MAB 11374B*
10	*C. multigeniculata*	**$n = 11$**	NV, Clark Co., McCullough Range, 8.5 km WSW of the summit of Black Mtn., 20 km SW of Henderson	31	35.8960° −115.1238°	975	*MAB 15152; MAB 15153; MAB 153033*
11	*C. multigeniculata*	**$n = 11$**	AZ, Mohave Co., Black Mts., 2.4 km NNW of Willow Spring, 33 km WNW of Kingman.	31	35.3168° −114.3870°	1200	***MAB 15257; MAB 15258; MAB 15262***
12	*C. acanthocarpa*	ND	CA, San Bernardino Co., 9 km WSW of South Pass, 32 km due W of Needles, just S of Interstate 40 (type locality for *C. acanthocarpa* var. *coloradensis* (L. D. Benson) Pinkava	30	34.8375° −114.9848°	670	*L. Benson 10375*
13	*C. acanthocarpa*	ND	CA, San Bernardino Co., 5 km ENE of Vidal Junction, 8 km S of Savahia Peak, lower bajada to the SW of the Whipple Mts.	30	34.1994° −114.5216°	295	*MAB 17718*
14	*C. acanthocarpa*	**$n = 11$**	CA, Imperial Co., 5 km NW of the N end of Cargo Muchacho Mts., 32 km NW of Yuma, AZ	30	32.9452° −114.8558°	190	***MAB 17541.1***
15	*C. acanthocarpa*	ND	CA, San Bernardino Co., Ivanpah Valley, 13 km NNE of the summit of Clark Mtn., 67 km SE of central Las Vegas	30	35.6040° −115.4600°	900	*MAB 17660*

TABLE 2. DESCRIPTION OF CHARACTERS MEASURED. Node is used here in reference to where branches originate from trunks or larger branches, not a stem node or areole.

Abbreviation	Character	Description
STEML	stem length (mm)	mean length of three ultimate mature stem segments
STEMDIA	stem diameter (mm)	mean diameter at widest portion of three ultimate mature stem segments
DBTRBRCH	distance between trunk branches (cm)	mean length of three inter-branch spaces along the main trunk or, if unavailable, those along primary branches
BRANPTRND	branches per trunk node	mean number of branches at each of three trunk nodes, if unavailable or not easily visible, those along primary branches
TUBL	tubercle length (mm)	mean length of top-most penultimate tubercle from three stem segments
TUBW	tubercle width (mm)	mean width of top-most penultimate tubercle from three stem segments
TUBH	tubercle height (mm)	mean height of top-most penultimate tubercle from three stem segments
NOCSP	central spine number	mean number of central spines per areole from tubercles as described above
NORSP	radial spine number	mean number of radial spines per areole from tubercles as described above
CSPL	central spine length (mm)	mean length of longest central spine per areole from tubercles as described above
RSPL	radial spine length (mm)	mean length of longest radial spine per areole from tubercles as described above
CSPTH	central spine thickness (0.01 mm)	mean thickness of longest central spine per areole from tubercles as described above
SHTH	central spine sheath thickness (0.01 mm)	mean thickness of the sheath of the longest central spine per areole from tubercles as described above

which were morphologically intermediate between *C. acanthocarpa* and *C. multigeniculata.*

Multivariate Analysis

Discriminant function analysis resulted in a 99.1% correct classification of individuals within their pre-assigned taxa (Table 3). A single individual pre-classified as *Cylindropuntia chuckwallensis* was assigned by the DFA as *C. echinocarpa,* and three were assigned as *C. multigeniculata.* All four groups were significantly different from each other at the $P = 0.001$ level (Table 4). Results from MANOVA indicated that mean values for seven of the 13 continuous morphological characters for *C. chuckwallensis* were significantly different from those of *C. echinocarpa* and *C. multigeniculata* (Table 5). Descriptive statistics for the multivariate dataset are presented in Table 6.

DISCUSSION

Results support the inclusion of western and eastern populations of *Cylindropuntia multigeniculata* within one taxon. Predicted group membership correctly classified all individuals within *C. multigeniculata* populations, including those of the western population (population 11). Since not a single *C. multigeniculata* individual was incorrectly classified as *C. echinocarpa,* the evidence clearly supports the inclusion of the western population within *C. multigeniculata.* Since Pinkava's (2000) hybrid hypothesis was based on the inclusion of these western populations under *C. echinocarpa,* there is little, if any, remaining evidence to support his hypothesis.

Cylindropuntia chuckwallensis possesses a unique combination of characters when compared to its closest morphological relatives. It does not, however, possess any characters that are unique within the genus. This observation, combined with its polyploid nature, especially in comparison to its non-polyploid relatives, suggests that *C. chuckwallensis* is an allopolyploid. Its morphology indicates that the majority of its chromosomes came from a species similar to *C. multigeniculata.* The range of tepal colors between plants and the red coloration of the styles and stigmas indicate that the remaining chromosomes may have been contributed by *C. acanthocarpa* or a similar extinct ancestor (Fig. 3). Because *C. chuckwallensis* is morphologically more closely allied to *C. multigeniculata,* it is likely that *C. multigeniculata* contributed a larger number of chromosome sets than did *C. acanthocarpa.* Thus, *C. chuckwallensis* may have originated as triploid hybrid resulting from an unreduced gamete from *C. multigeniculata* and a normal gamete from *C. acanthocarpa,* or possibly a tetraploid individual of *C. multigeniculata* hybridizing with a diploid *C. acanthocarpa* to form hybrid triploids. The triploid may then have produced two unreduced gametes that united to form the hexaploid *C. chuckwallensis.*

If *Cylindropuntia chuckwallensis* has not undergone extensive evolutionary changes since these hypothetical events, then its morphology would be expected to align loosely with the formula $(2M + 1A)/3 = C$, where $M =$ *C. multigeniculata*, $A =$ *C. acanthocarpa*, and $C =$ *C. chuckwallensis*. This assumes that the genetic effects are additive and that there are no threshold effects for the morphological characters sampled.

FIG. 2. Flower longitudinal sections (left images) and face views (right images) for: A., *Cylindropuntia acanthocarpa* (*M. A. Baker 17541.1*); B., *C. echinocarpa* (*M. A. Baker 17531*); C., pollen-sterile *C. chuckwallensis* (*M. A. Baker 17534*); pollen fertile D., *C. chuckwallensis* (*M. A. Baker 17525.6*); E., *C. chuckwallensis* (*M. A. Baker 17525.7*); F., *C. chuckwallensis* (*M. A. Baker 17535*), bar = 1 cm.

The mean values for each character from the morphological analysis were inserted into the formula, and the resulting values for only four characters of the hypothetical hybrid were well-aligned with those of *C. chuckwallensis*: branches per internode, central spine number, central spine thickness, and sheath thickness. The remaining nine characters were not a close match, which, combined with the occurrence of a pink style and gynodioecy, indicates that the origin of *C. chuckwallensis* is more complex than that of an allopolyploid of recent origin. Alternatively, the origin may be more recent and the genetic effects from hybridization not additive. However, non-additive genetic effects for morphological characters do not appear to be the normal situation in Cactaceae.

An allopolyploid origin is further supported by the occurrence of tetraploidy in its close relative *C. whipplei* (Engelm. & J. M. Bigelow) F. M. Knuth var. *enodis* (Peebles) Backeberg and by the occurrence of putative hybrids, i.e., morphological intermediates, between *C. multigeniculata* and *C. acanthocarpa* that have been observed in the field at more than one site by the authors and by Clokey (1943). The occurrence of tetraploidy suggests a history of unreduced gametes, and the occurrence of putative hybrids suggests that hybridization between *C. multigeniculata* and *C. acanthocarpa* is not only possible but also probably frequent.

An alternative to the allopolyploid hypothesis is that *Cylindropuntia chuckwallensis* is an autopolyploid of an extinct or as yet undiscovered ancestor. The geographical disjunction between populations of *C. chuckwallensis* and those of *C. multigeniculata*, its differing morphology, and its gynodioecy suggest that, whether *C. chuckwallensis* is an allopolyploid or autopolyploid, it originated in the distant past.

Similarities between the morphology of *Cylindropuntia chuckwallensis* and *C. echinocarpa* indicate the two species may have similar origins. Putative hybrids between *C. acanthocarpa* and *C. multigeniculata* are similar morphologically to *C. echinocarpa*, suggesting that *C. echinocarpa* may also be of hybrid origin. Regardless of its beginning, the large geographic and morphological range of *C. echinocarpa* suggests a distant origin and that it should not be treated as a nothospecies.

The coincidence of flower colors, hexaploidy, gynodioecy, and geographic proximity among *Cylindropuntia chuckwallensis*, *C. calmalliana*, *C. sanfelipensis*, and *C. wolfii* is remarkable and warrants further investigation. It is possible that the four species share a common ancestor, most likely equal or similar to *C. acanthocarpa*. Morphologically, both *C. calmalliana* and *C. sanfelipensis*, and to a lesser extent, *C. wolfii*, are much more similar to *C. acanthocarpa* than is *C.*

TABLE 3. CLASSIFICATION RESULTS OF DISCRIMINANT FUNCTIONS ANALYSIS: PREDICTED GROUP MEMBERSHIP; 99.1% OF ORIGINAL GROUPED CASES WERE CORRECTLY CLASSIFIED.

		Predicted group membership				
	Taxon	*C. chuckwallensis*	*C. echinocarpa*	*C. acanthocarpa*	*C. multigeniculata*	Total
By number of individuals	*C. chuckwallensis*	117	1	0	3	121
	C. echinocarpa	0	119	0	0	119
	C. acanthocarpa	0	0	120	0	120
	C. multigeniculata	0	0	0	92	92
By percentage of individuals	*C. chuckwallensis*	96.7	0.8	0	2.5	100
	C. echinocarpa	0	100	0	0	100
	C. acanthocarpa	0	0	100	0	100
	C. multigeniculata	0	0	0	100	100

chuckwallensis. This may indicate that they may have received a greater genetic input from *C. acanthocarpa* in comparison to that of *C. chuckwallensis*, that the hybridization/polyploidization events were greatly staggered in time, or that the genetic effects simply were not additive. Since, as far as we know, gynodioecy is lacking in *C. acanthocarpa*, the development of gynodioecy among the four hexaploids may have been selected for by inbreeding depression rather than as a result of mutually acquired genes.

Taxonomic Treatment

Cylindropuntia chuckwallensis M. A. Baker & M. A. Cloud-Hughes, sp. nov. (Figs. 2 and 3).—Type: USA, California, Riverside Co., Chuckwalla Mountains, along Corn Springs Wash, 2.5 km WNW of Corn Spring, 550 m (1830 ft) elev., 33.6327°N, 115.3527°W, 9 Apr 2012, *Marc A. Baker 17534 with Michelle A. Cloud-Hughes* (holotype: ASU; isotype: SD).

Generally low, densely branched shrubs mostly broader (to 2+ m) than tall (to 1+ m), trunks one to several, decumbent to ascending, occasionally erect; the bases of older individuals with a gray matting of dead stems and spines; spacing between branch whorls generally less than 3 cm long; branches mostly in whorls of four or more; mature ultimate stems mostly less than three times long ($\bar{x}$ = 56 mm) as wide ($\bar{x}$ = 23 mm); tubercles averaging 11 mm long and approximately as wide as high ($\bar{x}$ = 8 mm); central spines 4–10 ($\bar{x}$ = 7), averaging 27 mm long; radial spines 6–12 ($\bar{x}$ = 8), averaging 13 mm long or less than half the length of the centrals; often difficult to differentiate between radial and central spines; thickest central spine averaging 0.42 mm with a sheath averaging 0.65 mm wide; flowers 3–5 cm long, 4–6 cm broad, tepals 1.5–3 cm long, pale yellow-green to orange to purple-red; style 1.5–3.5 cm long, generally pale to dark pink-purple, at least distally, although very pale green in approximately 10% of individuals; filament color generally matching style color; fruits obovate to suborbicular, thin-walled, without pulp, 15–18 mm wide, 15–30 mm long, areoles 30–55, up to 15 thin spines per areole, drying the first year; seeds about 50, white, irregularly discoid, mostly smooth or faces slightly convex or faceted, 1.5 mm thick, 3 mm in diameter.

Etymology

The species is named for its occurrence primarily within the Chuckwalla Mountains.

Taxonomic Relationships

The habit of *Cylindropuntia chuckwallensis* most closely resembles that of *C. multigeniculata*, with individuals mostly broader than tall, older individuals with several trunks, short spaces between trunk nodes, and with several stems per trunk or branch node. Mean values for spine thickness in *C. chuckwallensis* are intermediate between those of *C. multigeniculata* and *C.*

TABLE 4. WILKS' LAMBDA FOR THE RESULTS OF DISCRIMINANT FUNCTIONS ANALYSIS.

Test of function(s)	Wilks' lambda	Chi-square	df	Sig.
1 through 3	0.007	2217.382	39	0.000
2 through 3	0.118	944.368	24	0.000
3	0.420	384.309	11	0.000

TABLE 5. CHARACTER MEANS BY SPECIES. Means in bold are significantly different ($P < 0.01$) from means of all other species.

Character	Species			
	C. multigeniculata	*C. chuckwallensis*	*C. echinocarpa*	*C. acanthocarpa*
Distance between trunk branches	**1.4**	**2.9**	**8.9**	**17.2**
Branches per trunk node	**5.5**	**4.5**	**2.4**	**1.8**
Stem length	**41.3**	56.0	57.6	**108.4**
Stem diameter	**16.4**	22.6	24.0	**25.9**
Tubercle length	**6.7**	**10.7**	**12.8**	**27.4**
Tubercle width	**3.4**	**7.8**	**6.3**	**7.0**
Tubercle height	**3.8**	**7.6**	**6.2**	**7.1**
Central spine number	6.6	7.0	7.3	7.5
Radial spine number	**6.5**	8.0	8.0	**9.9**
Central spine length	**20.8**	26.8	**25.7**	28.3
Radial spine length	**8.7**	13.3	13.5	**16.5**
Central spine thickness	**28.9**	**41.9**	**55.2**	**68.1**
Central spine sheath thickness	**49.1**	**65.2**	**89.4**	**108.4**

echinocarpa but are significantly different from both species. Tubercles in *C. chuckwallensis* are significantly wider and taller than those of the other two species (Tables 6 and 7). The styles and filaments in individuals of *C. chuckwallensis* are generally pale to dark pink-purple, at least distally, although very pale green in approximately 10% of individuals. *Cylindropuntia acanthocarpa* shares this character, at least in its filaments. Both *C. multigeniculata* and *C. echinocarpa* have white to pale green styles and filaments.

Distribution, Conservation, and Ecology

Populations of *Cylindropuntia chuckwallensis* occur primarily in the area of the Chuckwalla Mountains extending to the north side of the Chocolate Mountains, and the eastern base of the Orocopia Mountains (Salt Creek), with satellite populations in the Cottonwood and Eagle Mountains in Joshua Tree National Park. Although the total range is approximately 50 km north to south and 60 km east to west, recorded individuals are confined within isolated areas totaling approximately 3200 hectares or 32 km^2. Since our results estimate an average density of 2.5 individuals per hectare, a rough estimate for the total number of individuals within known populations is 3200 hectares × 2.5 individuals per hectare or 8000 individuals.

Individuals of *Cylindropuntia chuckwallensis* occur primarily between an elevational range of 400–1600 m in rocky, gravelly, sandy, and silty substrate on desert pavement and along washes and slopes of varying aspects and inclinations.

Vegetation associated with populations of *Cylindropuntia chuckwallensis* includes sparse to moderately dense desert scrub. Associated vascular plant species are listed by site in Table 8. The most commonly occurring vascular plant associates are *Ambrosia dumosa* (A. Gray) W. W. Payne, *Fouquieria splendens* Engelm., *Hilaria rigida* (Thurb.) Benth. ex Scribn., and *Simmondsia chinensis* (Link) C. K. Schneid., which occurred at all five data collection sites. *Ambrosia salsola* (Torr. & A. Gray) Strother & B. G. Baldwin, *Cylindropuntia echinocarpa, C. ramosissima, Echinocereus engelmannii, Eriogonum inflatum* Torr. & Frém., *Larrea tridentata* (Sessé & Moc. ex DC.)

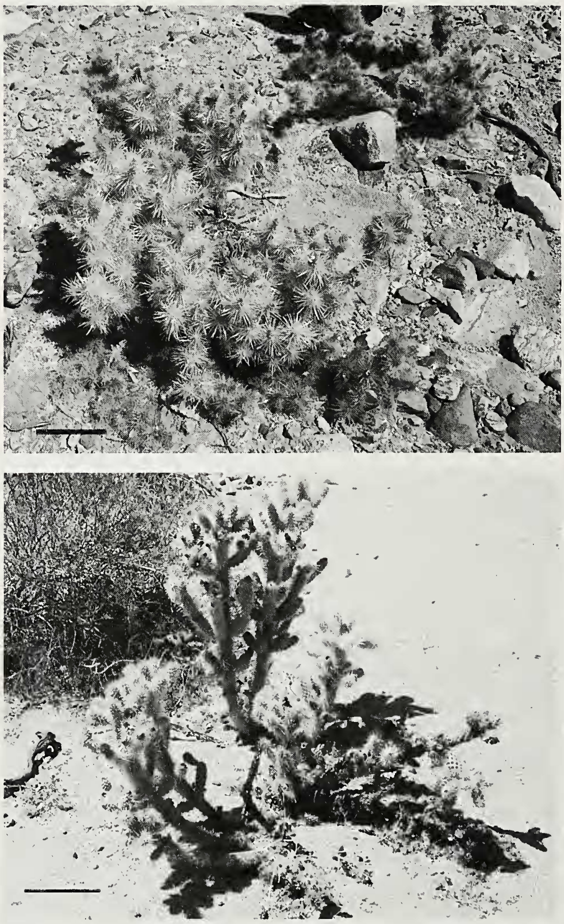

FIG. 3. Habit and habitat for *Cylindropuntia chuckwallensis*. Top image: *M. A. Baker 17534*; bottom image: *M. A. Baker 17535*, bar = 1 dm.

TABLE 6. DESCRIPTIVE STATISTICS FOR ALL SPECIES. Plant height (HT), plant width (W), primary branch angle (BANG), and internode length (IL) in cm; branches per internode (BPI), stem length (SL), stem diameter (SD), tubercle length (TL), tubercle width (TW), tubercle height (TH), number of central spines (CCN), number of radial spines (RSN), length of central spines (CSL), length of radial spines (RSL), thickness of central spines (CSTH), and thickness of sheaths (SHTH) in mm except for discrete characters.

Species	n	STATISTIC	HT	W	IL	BPI	SL	SD	TL	TW	TH	CCN	RPN	CSL	RSL	CSTH	SHTH
C. acanthocarpa	120	Minimum	46.0	50.0	5.3	1.0	54.3	18.0	17.0	4.7	4.0	3.3	5.3	15.7	9.0	0.45	0.65
		Maximum	219.0	322.0	34.7	3.7	224.7	36.7	39.0	11.0	10.3	14.0	14.3	42.3	25.3	1.06	1.65
		Mean	119.1	153.7	17.2	1.8	108.4	25.9	27.4	7.0	7.1	7.5	9.9	28.3	16.5	0.68	1.08
		95% CI Upper	125.1	162.9	18.2	1.9	112.9	26.7	28.3	7.3	7.3	7.8	10.2	29.2	17.1	0.7	1.12
		95% CI Lower	113.1	144.4	16.2	1.7	103.8	25.1	26.5	6.7	6.8	7.2	9.6	27.4	15.9	0.66	1.05
		Standard Dev	33.2	51.2	5.7	0.6	25.3	4.3	5.1	1.5	1.4	1.8	1.7	5.1	3.3	0.11	0.18
C. chuckwallensis	121	Minimum	24.0	10.0	0.5	2.0	33.0	16.7	7.3	5.3	4.3	4.0	5.7	17.3	8.3	24.7	39.0
		Maximum	153.0	239.0	7.0	7.7	96.7	28.7	15.7	10.3	10.3	10.0	11.7	41.0	27.7	59.3	94.0
		Mean	53.4	98.8	2.9	4.5	56.0	22.6	10.7	7.7	7.6	7.0	8.0	26.8	13.3	41.9	65.2
		95% CI Upper	57.2	106.5	3.1	4.7	58.1	23.1	11.0	7.8	7.9	7.3	8.2	27.6	13.8	43.2	67.0
		95% CI Lower	49.7	91.1	2.6	4.3	53.9	22.1	10.4	7.5	7.4	6.8	7.7	26.0	12.8	40.6	63.4
		Standard Dev	20.8	42.8	1.4	1.1	11.5	2.8	1.7	1.0	1.3	1.2	1.2	4.3	2.6	7.5	10.1
C. echinocarpa	119	Minimum	23.0	15.0	2.5	1.0	31.0	15.0	7.0	4.0	3.3	3.0	5.0	11.5	6.5	0.2	0.47
		Maximum	198.0	206.0	18.3	5.0	89.3	32.0	18.7	8.0	9.0	12.0	12.0	40.7	23.0	1.03	1.48
		Mean	77.4	85.0	8.9	2.4	57.6	24.0	12.8	6.3	6.2	7.3	8.0	25.7	13.5	0.55	0.89
		95% CI Upper	82.5	91.3	9.4	2.6	60.0	24.5	13.3	6.4	6.5	7.6	8.3	26.9	14.1	0.58	0.93
		95% CI Lower	72.2	78.7	8.4	2.3	55.2	23.4	12.4	6.1	6.0	6.9	7.7	24.4	12.9	0.52	0.86
		Standard Dev	28.4	34.6	2.8	0.9	13.1	3.1	2.7	0.9	1.3	1.8	1.7	6.9	3.3	0.15	0.19
C. multigeniculata	92	Minimum	21	19	0.5	2.3	20	11	3.7	2.6	2	3	2	10	5	0.17	0.25
		Maximum	98	402	3.7	8	60.7	24.3	10	5.7	5.7	13	10.7	37	13.6	0.46	0.87
		Mean	41.7	68.9	1.4	5.5	41.3	16.4	6.7	3.4	3.8	6.6	6.5	20.8	8.7	0.29	0.49
		95% CI Upper	44.6	79.8	1.5	5.8	43.2	17	7	3.5	3.9	7.1	6.8	21.8	9.1	0.3	0.52
		95% CI Lower	38.7	58	1.2	5.3	39.5	15.8	6.3	3.3	3.6	6.1	6.1	19.8	8.2	0.28	0.47
		Standard Dev	14.2	52.8	0.7	1.2	8.9	2.8	1.7	0.5	0.9	2.4	1.5	4.9	2	0.05	0.12

Table 7. Comparison of Diagnostic Characters among *Cylindropuntia chuckwallensis, C. echinocarpa,* and *C. multigeniculata.* Values for quantitative characters given as the range within 95% confidence levels.

Character	Species		
	C. chuckwallensis	*C. echinocarpa*	*C. multigeniculata*
Internode length	2.6–3.1cm	8.4–9.4 cm	1.2–1.5 cm
Branches per internode	4.3–4.7	2.3–2.6	5.3–5.8
Tubercle length	10.4–11.0 mm	12.4–13.3 mm	6.3–7.0 mm
Tubercle width	7.5–7.8 mm	6.1–6.4 mm	3.3–3.5 mm
Tubercle height	7.4–7.9 mm	6.0–6.5 mm	3.6–3.9 mm
Central spine thickness	0.40–0.43 mm	0.52–0.58 mm	0.28–0.30 mm
Sheath thickness	0.63–0.67 mm	0.86–0.93 mm	0.47–0.52 mm
Color of style and filaments	pale to dark pink-purple, at least distally, rarely very pale green	nearly white to pale green	nearly white to pale green
Gynodioecious	yes	no	no
Chromosome number	$n = 33$	$n = 11$	$n = 11$

Coville, *Parkinsonia florida* (Benth. ex A. Gray) S. Watson, and *Senegalia greggii* (A. Gray) Britton & Rose occurred at four of the five sites. Another cholla, *C. bigelovii*, occurred at three of the sites.

There are currently few if any conservation concerns associated with populations of *Cylindropuntia chuckwallensis*. No damage from off-road vehicles has been observed, and there seem to be no obvious herbivores other than those that eat the flowers and seeds.

Phenology

Flower buds of individuals of *Cylindropuntia chuckwallensis* emerge mid-March and anthesis occurs about four weeks later. Fruits generally mature about six to eight weeks after anthesis.

Paratypes: USA, California. **Riverside Co.:** Corn Spring, N side of Chuckwalla Mts., 33.6233°N, 115.3255°W, 17 Dec 2011, *M. A. Baker 17507 with M. A. Cloud-Hughes* (ASU); Corn Spring, N side of Chuckwalla Mts., 33.6257°N, 115.3284°W, 17 Mar 2013, *M. A. Cloud-Hughes 087* (RSA, SD); Corn Springs Wash, 830 m ENE of Aztec Spring, 33.6364°N, 115.3667°W, 19 Dec 2011, *M. A. Baker 17510 with M. A. Cloud-Hughes* (ASU); NE end of Chuckwalla Mts., 1.1 km W of Corn Spring Campground, 33.6246°N, 115.3381°W, 25 Mar 2012, *M. A. Baker 17525.1* (ASU, RSA); Same location, 25 Mar 2012, *M. A. Baker 17525.2* (ASU, SD); Same location, 25 Mar 2012, *M. A. Baker 17525.4* (ASU, US); Same location, 25 Mar 2012, *M. A. Baker 17525.5* (ASU, SD); Same location, 25 Mar 2012, *M. A. Baker 17525.6* (ASU, ASC); Same location, 25 Mar 2012, *M. A. Baker 17527.7 with M. A. Cloud-Hughes* (ASU, SD); Chuckwalla Mts., along Corn Springs Wash, 2.5 km WNW of Corn Spring, 33.6328°N, 115.3521°W, 9 Apr 2012, *M. A. Baker 17535 with M. A. Cloud-Hughes* (ASU, SD); Chuckwalla Mts., 500 m NW of Aztec Well, 33.6361°N, 115.3839°W, 15 Apr 2013, *M. A. Baker 17726* (ASU, RSA); Same location, 15 Apr 2013, *M. A. Baker 17727 with M. A. Cloud-Hughes* (US, SD); Chuckwalla Mts., vicinity of Corn Spring, , 33.62°N, 115.31°W, "dry slopes," 9 Apr 1922, *M. French Gilman s. n.* (RSA12621!); Chuckwalla Mts., vicinity of Corn Springs, 33.76°N, 115.37°W, 9 Apr 1922, *P. A. Munz 5017 with D. D. Keck*, box labeled "common on gravelly slopes, brown-red flowers" (UC409468!), sheet labeled "abundant about Aztec Well, on lower slopes, flowers reddish-brown" (POM11971!); along Salt Creek, 17.5 km WNW of Black Butte, 33.5866°N, 115.5521°W, 9 Apr 2012, *M. A. Baker 17533 with M. A. Cloud-Hughes* (ASU, UCR); N side of Chuckwalla Mts., 1 km west of Chuckwalla Spring, 33.4771°N, 115.2242°W, 1 May 2011, *M. A. Baker 17305* with *M. A. Cloud-Hughes, G. Rink, D. Robertson and N. Kramer* (ASU, RSA); N side of Chuckwalla Mts., 1.7 km NNE of Chuckwalla Spring, 33.4917°N, 115.2098°W, 9 Apr 2012, *M. A. Baker 17536* (ASU, RSA); Same location, 9 Apr 2012, *M. A. Baker 17536.1 with M. A. Cloud-Hughes* (ASU, US); Joshua Tree National Park, 5.5 km N of Cottonwood Spring, 33.7856°N, 115.8041°W, 20 Mar 2013, *M. A. Baker 17720.2* (RSA, JOTR); Same location, 20 Mar 2013, *M. A. Baker 17720.3 with M. A. Cloud-Hughes* (ASU); Cottonwood Mts., Joshua Tree National Park, 450 m SW of Cottonwood Spring, 33.7336°N, 115.8131°W, 20 Mar 2013, *M. A. Baker 17721.1 with M. A. Cloud-Hughes* (RSA, JOTR); Cottonwood Mts., Joshua Tree National Park, 450 m SW of Cottonwood Spring, 33.7338°N, 115.8134°W, 15 Apr 2013, *M. Harding 134 with M. A. Baker with M. A. Cloud-Hughes* (RSA, JOTR); Eagle Mts., Joshua Tree National Park, 7.3 km ENE of Cottonwood Spring, 33.7442°N, 115.7499°, 11 Apr 2013, *M. Harding 130* (JOTR!); Eagle Mts., Joshua Tree National Park, 5 km ENE of Cottonwood Spring, 33.7511°N, 115.7553°W, 11 Apr 2013, *M. Harding 132* (JOTR!); Cottonwood Mts., Joshua Tree National Park, Cottonwood Spring, 33.74°N, 115.81°W, 25 Apr 1928, *W. L. Jepson 12622b*

TABLE 8. LIST OF ASSOCIATED VASCULAR PLANT SPECIES FOR *CYLINDROPUNTIA CHUCKWALLENSIS*, BY SITE.

	Site				
Species	Chuckwalla spring	Indian well	Corn spring wash	Salt creek	Cottonwood canyon
Acamptopappus sphaerocephalus (Harv. & A. Gray) A. Gray		x			
Acmispon rigidus (Benth.) Brouillet					x
Adenophyllum porophylloides (A. Gray) Strother			x		x
Ambrosia dumosa (A. Gray) W. W. Payne	x	x	x	x	x
Ambrosia salsola (Torr. & A. Gray) Strother & B. G. Baldwin		x	x	x	x
Bahiopsis parishii (Greene) E. E. Schill. & Panero					x
Bebbia juncea (Benth.) Greene	x	x			x
Coryphantha alversonii (J. M. Coult.) Orcutt					x
Coleogyne ramosissima Torr.					x
Cylindropuntia bigelovii (Engelm.) F. M. Knuth	x	x	x		
Cylindropuntia echinocarpa (Engelm. & J. M. Bigelow) F. M. Knuth	x	x		x	x
Cylindropuntia munzii (C. B. Wolf) Backeb. (pro hybr.)		x			
Cylindropuntia ramosissima (Engelm.) F. M. Knuth	x	x	x		x
Ditaxis lanceolata (Benth.) Pax & K. Hoffm.			x		
Ditaxis neomexicana (Müll. Arg.) A. Heller			x		
Echinocactus polycephalus Engelm. & J. M. Bigelow	x	x			
Echinocereus engelmannii (Parry ex Engelm.) Lem.	x	x	x		x
Encelia farinosa A. Gray ex Torr.	x	x	x		x
Ephedra californica S. Watson		x		x	
Ephedra nevadensis S. Watson	x		x		x
Eriogonum inflatum Torr. & Frém.	x	x	x		x
Eriogonum fasciculatum Benth.					x
Euphorbia polycarpa Benth.	x		x		
Euphorbia setiloba Engelm. ex Torr.			x		
Fagonia laevis Standl.	x		x		
Ferocactus cylindraceus (Engelm.) Orcutt	x		x		x
Fouquieria splendens Engelm.	x	x	x	x	x
Funastrum hirtellum (A. Gray) Schltr.			x		
Hibiscus denudatus Benth.	x				
Hilaria rigida (Thurb.) Benth. ex Scribn.	x	x	x	x	x
Hyptis emoryi Torr.	x		x		
Krameria bicolor S. Watson					
Krameria erecta Willd. ex Schult.	x	x	x		x
Larrea tridentata (Sessé & Moc. ex DC.) Coville	x	x	x	x	
Lycium andersonii A. Gray	x	x	x		
Mammillaria tetrancistra Engelm.	x		x		
Marina parryi (Torr. & A. Gray) Barneby			x		
Mirabilis laevis (Benth.) Curran					x
Olneya tesota A. Gray	x	x	x		
Opuntia basilaris Engelm. & J. M. Bigelow			x		x
Parkinsonia florida (Benth. ex A. Gray) S. Watson	x		x	x	x
Peucephyllum schottii A. Gray	x				
Phoradendron californicum Nutt.		x	x		
Porophyllum gracile Benth.		x	x		
Psorothamnus schottii (Torr.) Barneby	x	x			
Psorothamnus spinosus (A. Gray) Barneby			x		
Scutellaria mexicana (Torr.) A. J. Paton		x			x
Senegalia greggii (A. Gray) Britton & Rose	x	x	x		x
Senna armata (S. Watson) H. S. Irwin & Barneby		x			x
Simmondsia chinensis (Link) C. K. Schneid.	x	x	x	x	x
Sphaeralcea ambigua A. Gray		x			x
Stephanomeria pauciflora (Torr.) A. Nelson		x	x		
Tetracoccus hallii Brandegee			x		x
Trixis californica Kellogg			x		x
Yucca schidigera Ortgies				x	x
Ziziphus obtusifolia (Hook. ex Torr. & A. Gray) A. Gray		x			

(JEPS66875 digital image!); Cottonwood Mts., Joshua Tree National Park, near Cottonwood, 33.74°N, 115.81°W, 8 May 1971, *J. R. Shevock 1035* (RSA303531!); Cottonwood Mts., Joshua Tree National Park, hills N and NE of Cottonwood Spring, "Flowers a peculiar dull reddish purple, sometimes with a yellowish shade," 33.74°N, 115.81°W, 24 Apr 1928, *F. W. Peirson 7901* (RSA65624!); Cottonwood Mts., Joshua Tree National Park, Cottonwood Road, "quartz outcrop," 915 m (3000 ft) elev., 21 May 1941, *J. E. Cole 763* (JOTR1119!) (The specimen includes a single flower with dark purple-red stamen filaments and tepals. According to Mitzi Harding (pers. comm. 2013), this locality corresponds to hillside overlain with quartz gravel and rocks 1 km west of Smoke Tree Wash, 5.5 km N of Cottonwood Spring, 945 m [3100ft]); **Imperial Co.:** S side of Chuckwalla Mts., 3.8 km SW of Graham Pass, 33.4271°N, 115.1492°W, 10 Apr 2012, *M. A. Baker 17537 with M. A. Cloud-Hughes* (ASU, UNLV); S side of Chuckwalla Mts., along Graham Pass Road, 1.7 km E of its intersection with Bradshaw Trail, 33.4263°N, 115.1532°W, 20 Mar 2013, *M. A. Baker 17719.1* (ASU, RSA); Same location, 20 Mar 2013, *M. A. Baker 17719.2* (ASU, SRSC); Same location, 20 Mar 2013, *M. A. Baker 17719.3* (ASU, SD); Same location, 20 Mar 2013, *M. A. Baker 17719.4 with M. A. Cloud-Hughes* (ASU, UCR).

KEY TO THE SPINY-FRUITED *CYLINDROPUNTIA* OF THE UNITED STATES

Varieties of *Cylindropuntia acanthocarpa* and *C. californica* are not treated here. Morphological intermediates between *C. acanthocarpa* and *C. echinocarpa*, *C. ganderi* and *C. californica*, and *C. echinocarpa* and *C. californica* are common in areas of sympatry.

1\. Ultimate mature stem segment less than 1 cm in diameter, tubercles less than 1–2 mm high. . . . . *Cylindropuntia ramosissima*

1′. Ultimate mature stem segment greater than 1.5 cm in diameter, tubercles greater than 1–2 mm high

2\. Ultimate mature stem segments generally less than 10 cm long, tubercles less than three times long as wide

3\. Generally erect shrubs (except when infested by rodents), generally with a single ascending to erect main trunk, distance between trunk nodes generally at least 10 cm long, generally with one or two branches per trunk node . . . . *Cylindropuntia echinocarpa*

3′. Generally low shrubs, generally with several decumbent to ascending main trunks, distance between trunk nodes generally less than 5 cm long, generally with three or more branches per trunk node

4\. Style and stamen filaments generally with at least some purple-pink coloration; inner tepals pale orange-yellow to purple-red, fruits always very spiny and drying within a few weeks, Riverside and Imperial counties, California. . . . . *Cylindropuntia chuckwallensis*

4′. Style and stamen filaments with no purple-pink coloration, inner tepals always pale green-yellow; fruits often not heavily spined, at least for westernmost populations, not drying for several months or more, perhaps drying more quickly in easternmost populations, Clark County, Nevada and Mohave County, Arizona. . . . . *Cylindropuntia multigeniculata*

2′. Ultimate mature stem segments generally more than 10 cm long, tubercles more than three times long as wide

5\. Erect open shrubs, generally with a single ascending to erect main trunk that branches well above the base . . . . *Cylindropuntia acanthocarpa*

5′. Mostly matted shrubs, older individuals generally with several main trunks that branch near or below the base of the plant

6\. Stamen filaments purple-red, inner tepals orange-yellow to purple-red, stems very stout, generally greater than 4 cm diameter, areoles of older stems with proliferating spines — narrowly endemic to extreme southeastern San Diego and extreme southwestern Imperial counties, California . . . . *Cylindropuntia wolfii*

6′. Stamen filaments pale yellow-green, inner tepals yellow to green-yellow, stems thin, generally less than 2.5 cm diameter, areoles of older stems occasionally with proliferating spines — widespread from coastal mountains and nearby deserts of southwestern California.

7\. Spines not overlapping or only slightly overlapping those of adjacent areoles, fruits weakly spined, coast and coastal mountains, southern California . . . . *Cylindropuntia californica*

7′. Spines overlapping those of adjacent areoles for half their length or more, fruits strongly spined, deserts of eastern San Diego, western Imperial, and south edge of Riverside counties, California . . . . *Cylindropuntia ganderi*

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